Mitt. Bayer. Staatsslg. Paläont. hist. Geol.	38	227–242	München, 15. 12. 1998

Propagation of Cracks and Structural Reinforcement in the Enamel of Arvicolid Molars (Mammalia, Rodentia)

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With 19 figures

Abstract

Various crack patterns in the dental enamel of the lower first molars (M_1s) of the fossil and recent arvicolid rodents are studied. This work demonstrates the presence of various premortem and postmortem cracks in the enamel and its 2-D effect in different types of enamel patterns, viz., radial enamel, tangential enamel and lamellar enamel in the M_1s of arvicolids. The study suggests that the vertical cracks propagating across the molars are effectively stopped only by lamellar enamel which provides the best reinforcement against such cracks. Radial enamel and tangential enamel fail to stop or divert such kind of cracks produced in the enamel. A qualitative as well as quantitative development of lamellar enamel has been observed throughout the evolutionary history of arvicolid rodents. The lamellar enamel is found to occupy the minimum portion of total enamel area of the M_1s of *Kilarcola indicus* (2,4 Ma in age) and maximum in the recent arvicolids such *as Microtus juldaschi, M. sikimensis* and *Alticola roylei*. Radial enamel has been found to be quantitatively highly developed in *Kilarcola* but in later genera viz., *Alticola* and *Microtus*, it is found to be restricted to the push sides of cutting edges. This kind of pattern may be significant as far as the type of food and dietary diversity is concerned.

Kurzfassung

Unterschiedliche Belastungsstrukturen im Zahnschmelz der ersten Unterkiefermolaren (M_1s) fossiler und rezenter arvicolider Rodentier wurden untersucht. Die Existenz verschiedener prä- und postmortaler Frakturen im Schmelz und deren 2-D-Effekt unterschiedlicher Schmelzmuster, radialer Schmelz, tangentialer Schmelz und lamellärer Schmelz, der M_1 von Arvicoliden wird dargestellt. Anhand der Untersuchungen läßt sich rückschließen, daß Längsfrakturen an Molaren effektiv nur vom lamellären Schmelz gestoppt werden. Radiale und tangentiale Schmelzstrukturen können solche Belastungen hingegen weder aufhalten noch ableiten. Sowohl eine quantitative als auch qualitative Entwicklung lamellärer Schmelzstrukturen konnte für die Entwicklungsgeschichte arvicolider Rodentier beobachtet werden. Der Minimalteil von lamellären Schmelzstrukturen am Gesamtschmelzaufkommen der M_1 fand sich bei *Kilarcola indicus* (2,4 Ma alt), der Maximalanteil bei rezenten Arvicoliden wie

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Microtus juldaschi, M. sikimensis und *Alticola roylei*. Radiale Schmelzstrukturen wurden in mengenmäßig hoher Beteiligung bei *Kilarcola*, nicht aber bei nachfolgenden Gattungen wie *Alticola* und *Microtus* gefunden und an den Druckzonen der Schneidekanten nachgewiesen. Diese Muster mögen als aussagekräftig, sowohl für die Art als auch das Spektrum der Nahrung gelten.

Introduction

Mammalian dental enamel demostrates the biological advantages of hardness and wear resistance in occlusal plane. Enamel takes most of the pressure and load exerted on the occlusal surface (Boyde, 1989), and hence shows its functional significance. But, the enamel is a brittle material and due to the brittleness, it requires the presence of underlying dentine to transmit and dissipate the occlusal forces (Boyde, 1985; Ten Cate, 1989; Lin & Douglas, 1994).

Scanning electron microscope studies of mammalian dental enamel have showed various kinds of enamel microstructure in different groups of mammals. This variation is mainly due to the difference in the arrangement of enamel prisms which are bundles of fibres of apatite crystallites (Boyde et al. 1988; Pfretzschner 1988).

Complexities in the microstructure of mammalian dental enamel have been studied in detail by various workers (lately by Koenigswald & Clemens, 1992; Rensberger & Pfretzschner, 1992; Martin 1993; Srivastava, 1993 and Koenigswald et al. 1994). Several attempts are made to understand the functional significance of complexities in mamalian dental enamel (Rensberger, 1973, 1992, 1993, 1995a, 1995b; Pfretzschner, 1994; Hojo, 1996,; Srivastava et al. ms.). The role of Hunter Schreger Bands (HSB) in mammalian dental enamel has clearly been indicated by Koenigswald et al., (1987). The HSBs appear in longitudinal section of dental enamel as bands of decussating prisms of apatite crystallites. The crystallites of Interprismatic Matrix (IPM) in HSBs may follow the prisms or may be in right angles to the decussating bands of the prisms. The HSBs are interpreted as strengthening devices which prevent propagation of hairline cracks at higher load conditions. The enamel microstructure and arrangement of HSBs vary in different groups of mammals (Koenigswald & Clemens, 1992). The rodent incisor enamel possesses the most derived and complicated microstructure among all the mammals. The presence of HSBs in rodents is the only exception to the general observation of absence of HSBs in small mammals (Koenigswald, 1985; Koenigswald et al. 1987).

In the rodent incisors, the enamel is an outer layer which covers the dentine only from the anterior side. The HSBs occupy the inner half (i.e, towards the enamel and dentine junction) of the total enamel thickness (Portio Interna) and are at steep angles to the Enamel-Dentine Junction (EDJ). The outer enamel (Portio externa) lack HSBs and instead there is a radial enamel in which the long axes of the enamel prisms are oriented radially from the EDJ as seen in a horizontal plane and the prisms rise occlusally towards the enamel surface as seen in a vertical plane (Koenigswald & Clemens, 1992). The radial enamel characterises the cutting edge of the enamel (= tip of the incisors) also, where the HSBs may be worn away due to continuous wear of the evergrowing incisors of the rodents. This kind of 'schmelzmuster' (three dimensional arrangement of one or several different enamel types in the enamel band) can be observed in most of the rodent families except the family Arvicolidae.

The members of the Arvicolidae (voles and lemmings) possess slightly different arrangement of prisms in their dental enamel.

Arvicolids in general are characterised by having one slender incisor and three hypsodont (high crowned) and rootless molars in both upper and lower jaws. At least five lineages (Lemminae, Dicrostonychinae, Lagurinae and *Arvicola* and *Microtus*) possess rootless molars, however a few less derived genera such as *Ellobius or Prometheomys, Clethrionomys, Mimomys, Kilarcola* etc. possess rooted molars (Kotlia & Koenigswald 1992, Koenigswald et al., 1994).

The enamel in the arvicolid incisors is characterised by highly specialised uniserial enamel (Koenigswald et al., 1994), in which one prism wide HSBs occupy the portio interna, and the radial enamel occupies the portio externa. In fact, most of the myomorphs and sciuromorphs in the extant fauna are characterised by the uniserial HSBs (Koenigswald et al. 1993).

Arvicolid molars differ from most of the cricetids and murids in possessing a very complex Schmelzmuster (Koenigswald 1980, 1982). The molars are characterised by deep re-entrant folds of synclines separating the occlusal surface into alternating dentine triangles with enamel bands. In the lower molars, the dentine triangles have a concave mesial side and a convex distal side. According to propalinal movement of the jaw during mastication, the chewing forces meet the dentine triangles in the lower jaw from the concave mesial side which is termed as the leading edge. The convex distal side is known as trailing edge. The leading edge is composed of inner lamellar enamel (uniserial HSBs) and outer radial enamel. In contrast to this, the trailing edge possesses inner radial enamel and outer tangential enamel (Koenigswald, 1980, 1982; Kotlia & Koenigswald, 1992).

Lamellar enamel is composed of single layered HSBs (one prism wide HSBs, the uniserial HSBs) parallel to the chewing surface. Prisms of one band cross the prisms of neighbouring bands at right angles. The interprismatic matrix is also present between the prisms which strengthens the enamel in the third direction (Koenigswald, 1980).

In radial enamel, the prisms have parallel orientation and form a steep angle with the chewing surface. The interprismatic matrix crosses prisms approximately at right angles. In tangential enamel, the arrangement of prisms is like that of in the radial enamel but the prisms in the former are arranged parallel to the chewing surface.

The arvicolid enamel pattern is closely related to the stress pattern during mastication (Koenigswald 1977, 1980, 1982). The leading edge and apex of dentine triangles bear most of the stresses during mastication. Hence, the enamel pattern in the leading edge and at the apex of the dentine triangles is such that they can withstand various tensile stresses. These tensile stresses may be responsible for the development of cracks perpendicular to them (Koenigswald et al., 1987).

The objective of the present work is to study the nature and propagation of cracks in various enamel bands of arvicolid molars and to analyse the behaviour of different enamel patterns.

Prior to this study, the functional properties of lamellar enamel and radial enamel in arvicolid molars have been discussed by Koenigswald & Martin (1984). The crack stopping mechanism of lamellar enamel has also been suggested by various workers (Koenigswald & Pfretzschner, 1987, 1991; Pfretzschner, 1988, 1994). The present paper provides data on the arvicolids, recently described by Kotlia & Koenigswald (1992).

We have observed that the premortem vertical cracks across the tooth (in first molars) are affected only by the lamellar enamel. Wherever lamellar enamel appears, the cracks are either stopped or diverted into another direction. In contrast to this, where tangential or radial enamel is present, the cracks travel throughout the enamel width without much hindrance or diversion from their original path.

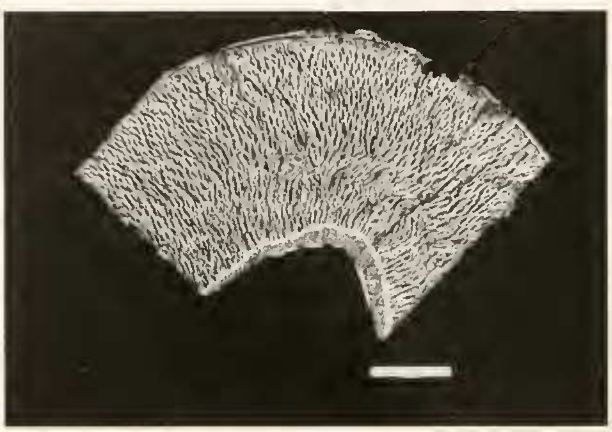
Materials and Methods

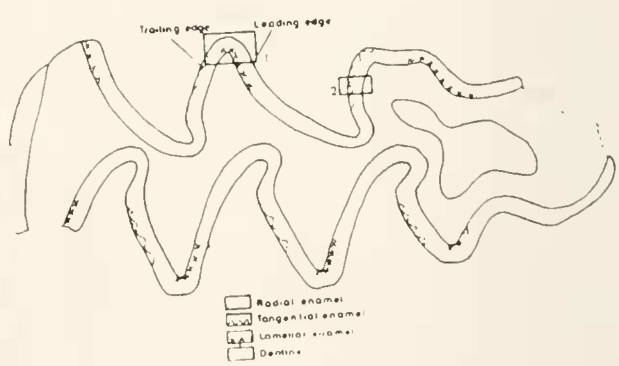
The fossil as well as recent arvicolids of different ages are studied. The material for the present study comprises the first lower molars of *Kilarcola indicus* (No. KH/146, 2,4 Ma in age), *K. indicus sahnii* (No. KH/157, 2,4 Ma), *K. kashmiriensis* (No. KH/719, 1,6 Ma), *Alticola roylei* (No. 64A, recent), *Microtus juldaschi* (No. 4973, recent) and *M. sikimensis* (No. 5091, recent).

The horizons yielding *Kilarcola indicus* and *K. kashmiriensis* have been dated to 2,4 Ma and 1,5 Ma (KOTLIA & KOENIGSWALD 1992; KOTLIA & SAHNI 1993, KOTLIA, 1994). *Microtus juldaschi, M. sikimensis* and *Alticola roylei* are the recent forms studied by us. A detailed phylogeny of the studied genera using cladistic analysis and constructing a cladogram was done by KOTLIA & KOENIGSWALD (1992). The analysis approves the stated phylogenetic relationships among the arvicolid genera.

The specimens were embedded in artificial resin and polished on the occlusal surface. After polishing, the specimens were very briefly etched with 2N hydrochloric acid for 2-3 seconds to make the internal structure of the enamel of fossil molars visible. The treatment was done taking full care that the process does not affect original crack patterns (premortem crack patterns). For recent arvicolid molars, a brief etching with hydrogen peroxide was found to be effective. The teeth were then gold coated to make the surface conducting. The microstructure of the dental enamel was observed under the Scanning Electron Microscope (SEM) at various magnifications ranging between 100 - 10.000.

The material under study is catalogued in the paleontological laboratory, Geology Department, Kumaun University, Nainital under the possession of the second author.





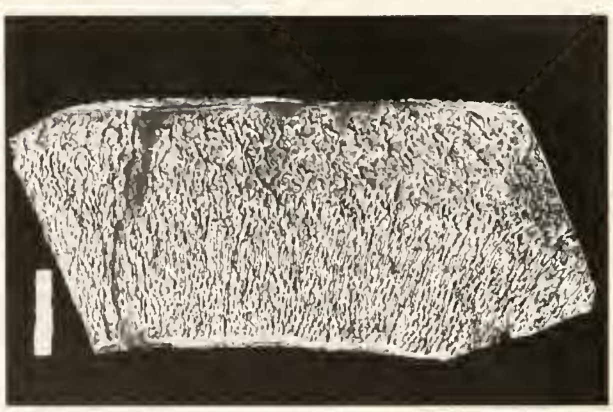


Fig. 1: Occlusal view of polished and etched enamel band of *Kilarcola indicus*. The presence of outer radial enamel and inner discrete lamellar enamel is clearly visible on anticline and leading edge. Most of the cracks travel throughout the thickness of radial enamel and are stopped only in discrete lamellar enamel. Bar = 30 µm.

Fig. 2: Occlusal view of polished and etched enamel band of M_1 of *Kilarcola indicus*. The trailing edge is occupied by tangential enamel on the outer side and redial enamel on the inner side. The outer tangential enamel and the inner radial enamel do not provide reinforcement against the vertical cracks. The cracks travel throughout the width of the enamel band without any hindrance.

Observations

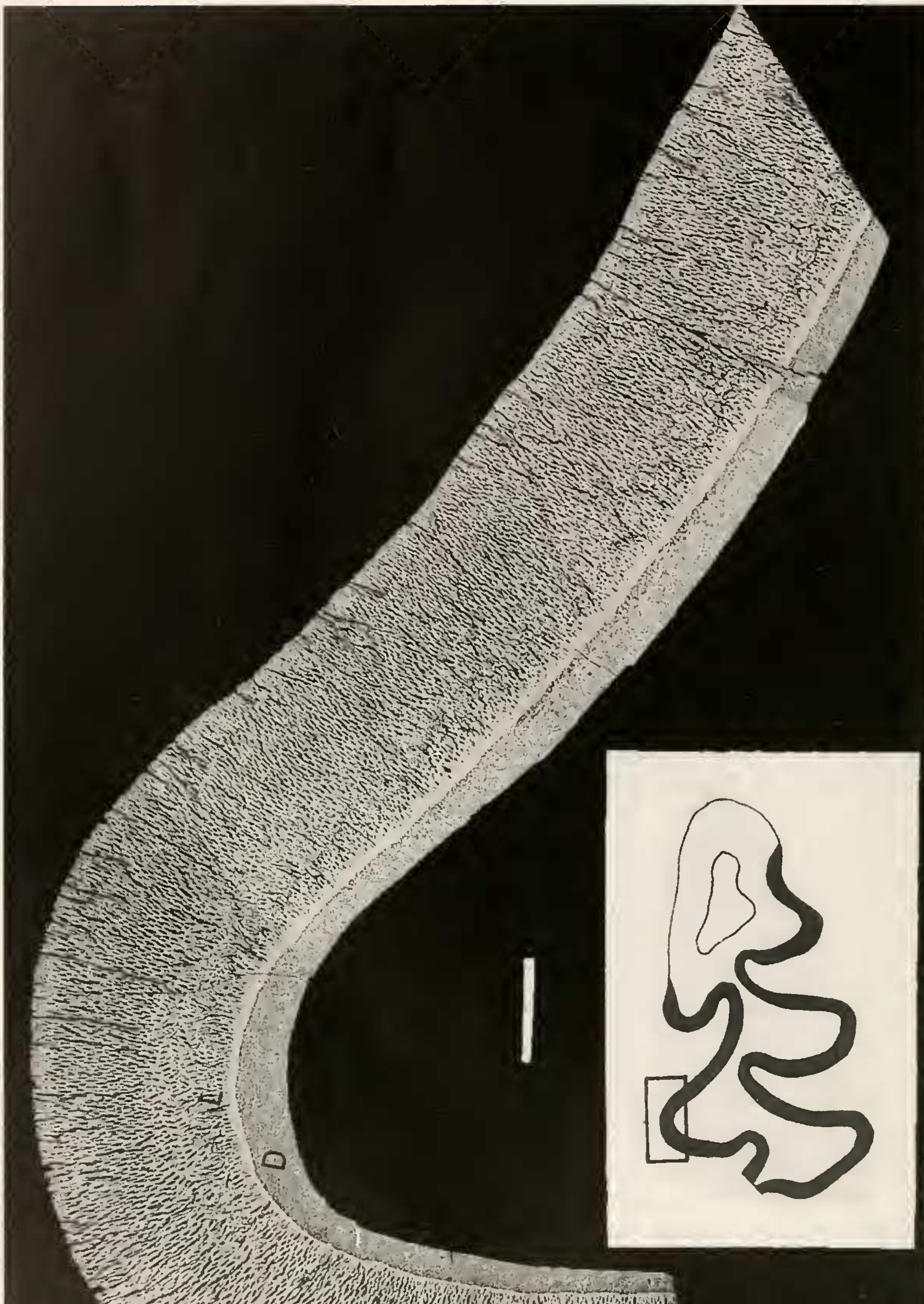
Various hairline cracks have been observed in lower first molars of various genera of arvicolid rodents. Most of the cracks are assigned to that of premortem origin. The cracks are mostly concentrated in the area of molar anticline and around the leading edge (postmortem cracks are randomly distributed); they show worn and rounded edges possibly resulting from chewing abrasion (RENSBERGER, 1987). The postmortem cracks caused by post burial stress concentrating impacts are mostly hertzian cracks, median cracks or lateral cracks (RENSBERGER, 1987) whereas drying of teeth produces cracks oriented in different directions just like mud cracks and other shrinkage cracks (RENSBERGER, 1987). In arvicolid molars, postmortem cracks are found to be absent. However a few thick cracks and the cracks originating from dentine side are assigned to that of postmortem origin (discussed elswhere in the text).

In *Kilarcola indicus*, the leading edges comprise radial enamel on the outer side. On the inner side as well as on dentine triangles and around the *Mimomys*-Kante (*Mimomys* edge on the anterior loop), lamellar enamel is present which extends into leading edges for a short distance. The lamellar enamel occupies about one third of the total thickness of the enamel on the apex of the dentine triangles and comparatively more around the *Mimomys*-Kante. The trailing edges are mostly occupied by the radial enamel. The primitive outer tangential enamel occupies between one-forth and half of the enamel thickness. The posterior loop is mainly composed of radial enamel of about 30-40% outer primitive tangential enamel. Occasionally, the tangential enamel is overlain by a thin layer of radial enamel. The enamel pattern in the subspecies *K. indicus sahnii*, is similar to that in *K. indicus*. The leading edge is made up mainly of radial enamel and the trailing edge consists of radial and tangential enamel. This simply constructed enamel pattern is called as 'isoknem enamel pattern' (KOTLIA & SAHNI, 1993). Discrete (not fully developed) lamellar enamel is present on the apices of the anticlines, extending for a little into the leading edges.

We observe that the cracks oriented vertically to the occlusal surface in the M_1s of *Kilarcola indicus* affect the radial enamel mostly on the dentine triangles and leading edges. The cracks as can be seen in figs. 1 & 2, travel throughout the radial enamel without changing much of their direction of propagation. It is significant to note here that the cracks do not divert from their initial direction of propagation. They follow an interprismatic path along the prisms' boundary on the chewing surface. In case of comparatively thicker cracks (postmortem artificial cracks, fig. 2), they travel straight without discriminating between prisms and prism boundaries (as the magnitude of tensile stresses exceeds the tensile strength of the enamel prisms). In fig. 1, a crack apparently originating from the inner side of enamel follows a path along prisms' boundary in discrete lamellar enamel. The cracks which originate from the inner side of tooth, i.e., from inner dentine, are not common and are very unusual (postmortem artificial cracks). Discrete lamellar enamel shows least measure to protect the tooth from such cracks. In the subspecies *K. indicus sahnii*, a number of hairline cracks can be observed originating from outer radial enamel. In radial enamel, the cracks do not meet any reinforcement pattern and thus extend throughout the thickness of radial enamel and travel deep up to the discrete lamellar enamel. They are stopped only at discrete lamellar enamel (fig. 3).

In *Kilarcola kashmiriensis*, the Schmelzmuster is made up mainly of radial enamel. Lamellar enamel is well developed on the apex of dentine triangles occupying more than one-third of the total enamel thickness. It extends in the form of discrete lamellar enamel for more than half way on the leading edge. The trailing edge possesses an inner radial enamel and occasional an outer tangential enamel. Tangential enamel begins near the apex and extends more than half way into the trailing edges.

Vertical cracks across the molars are well developed on the apex of the dentine triangles and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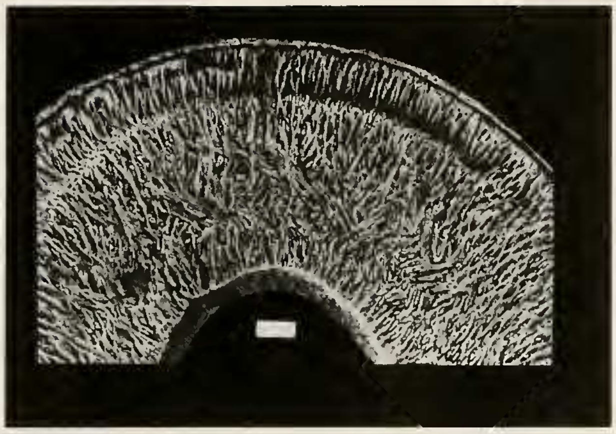

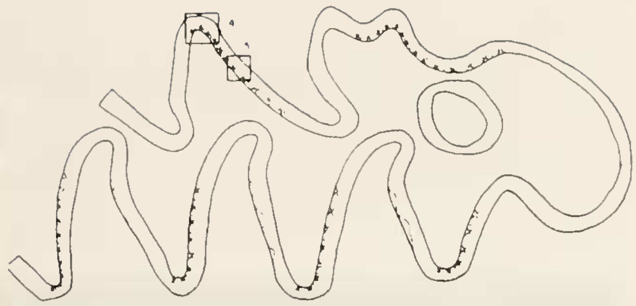

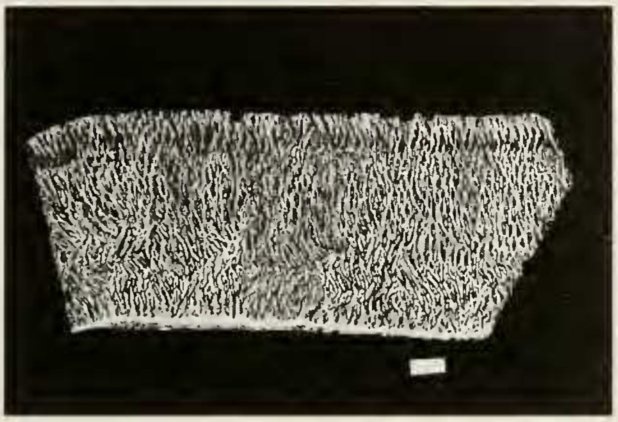

Fig. 4: Occlusal view of polished and etched enamel band on anticline of M_1 of *Kilarcola kashmiriensis* showing a progressive development of schmelzmuster in phylogenetic sequence. The radial enamel is present on the outer margin and discrete lamellar enamel on the inner margin. The vertical cracks in lamellar enamel are soon stopped due to change in their original direction of propagation. The outer false layer in the radial enamel is due to the Retzius lines and does not show any structural significance. Bar = 10 µm.

Fig. 5: Occlusal view of polished and etched enamel band in leading edge in M_1 of *Kilarcola kashmiriensis*. The radial enamel is present in the outer portion and discrete lamellar enamel is present in the inner portion of the enamel band. Several hairline cracks cross the radial enamel and reach to the lamellar enamel where they are stopped by the HSBs. Bar = 10 µm.

leading edge (figs. 4 & 5). They travel throughout the radial enamel without much deviation of their initial direction of propagation. As soon as the cracks reach lamellar enamel, they turn in the direction of the prisms' orientation and follow different directions forming inverted 'Y' shaped patterns (fig. 4). On the other hand such cracks do not meet lamellar enamel on trailing edges and hence travel throughout the thickness of enamel.

Microtus juldaschi shows highly developed and modified lamellar enamel which occupies around two-thirds of the inner side of total enamel thickness on the apex of the dentine triangles. The remaining outer one-third is occupied by radial enamel. On the trailing edges,

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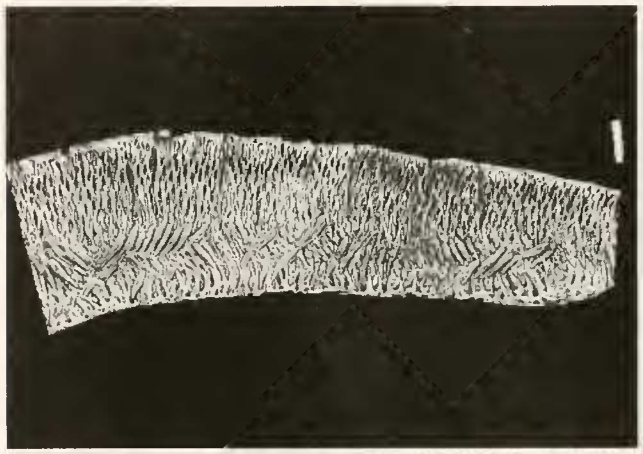
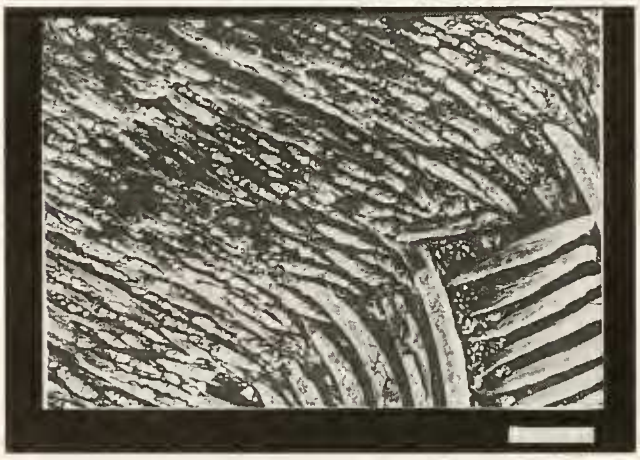
Fig. 3: Occlusal view of polished and etched enamel band of M_1 of *Kilarcola indicus sahnii*. The radial enamel occupies the outer portion of enamel at the summit of the anticline and in the leading edge; the inner portion of enamel is occupied by discrete lamellar enamel. In the trailing edge the radial enamel occupies the inner portion of the enamel, whereas the outer portion is occupied by tangential enamel. Several vertical hairline cracks travel through the enamel band which are stopped only by discrete lamellar enamel. The cracks of high intensity (artificial cracks created by grinding process) are neither affected by radial enamel and tangential enamel nor by lamellar enamel. D = dentine, R = radial enamel, T = tangential enamel, L = lamellar enamel. Bar = 30 µm.

radial enamel changes its position to the inner margin and occupies half of the total enamel thickness. The remaining half is occupied by tangential enamel.

The vertical cracks in M_1s of *Microtus juldaschi* travel straight in radial enamel, and as they reach lamellar enamel they follow the direction of lamellar enamel prisms. When they enter a lamellar enamel band, which is parallel to the direction of cracks, they follow the bands' direction and damage the enamel until they meet a decussating band (fig. 6). The cracks which are several HSBs wide are split up into two components by HSBs (figs. 7 & 8). These crack components are inclined to the tension forces and therefore stop soon (Koenigswald et al. 1987).

In *Microtus sikimensis*, the inner lamellar enamel occupies about 50% of the total enamel thickness throughout the leading edge and about 70% near the apices of the dentine triangles (Kotlia & Sahni, (1993). When compared to *M. juldaschi*, the lamellar enamel penetrates more deeply into the trailing edge in *M. sikimensis*. The radial enamel is well developed on synclines and trailing edges but is incipient on the posterior loop. The outer tangential enamel is





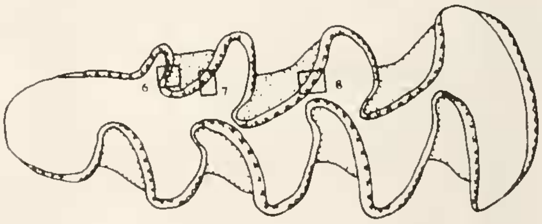


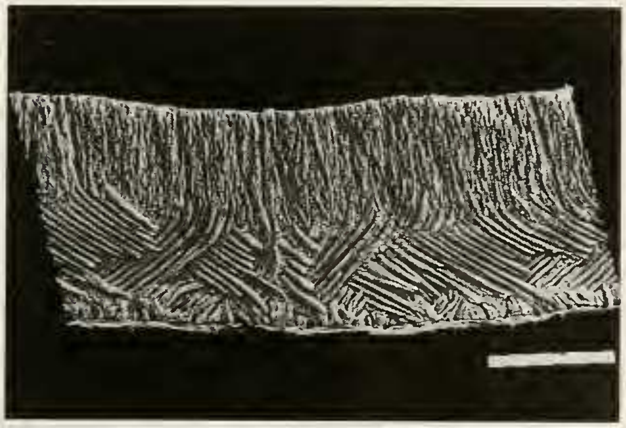
Fig. 6: Occlusal view of polished and etched enamel band in M_1 of *Microtus juldaschi*. The vertical cracks do not cross the lamellar enamel, whereas they travel throughout the thickness of the radial enamel. Bar = 10 µm.

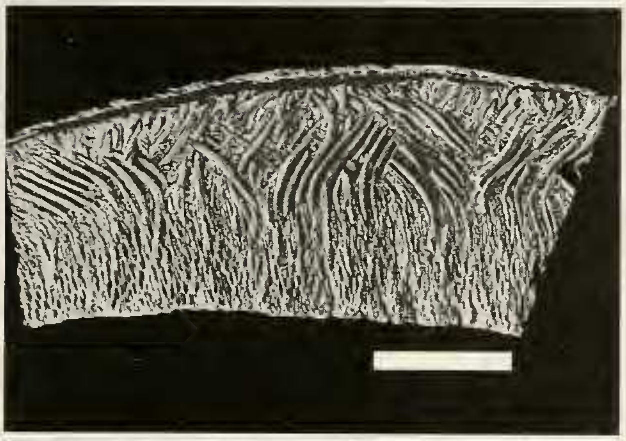
Fig. 7: Occlusal closer view of polished and etched enamel band in the leading edge of M_1 of *Microtus juldaschi* showing propagation of a crack in the radial enamel. As soon as the crack reaches the lamellar enamel it meets a decussating band which makes an angle with the direction of the crack. The crack stops due to a change in the direction of its propagation and it does not extend in the lamellar enamel. Bar = 10 µm.

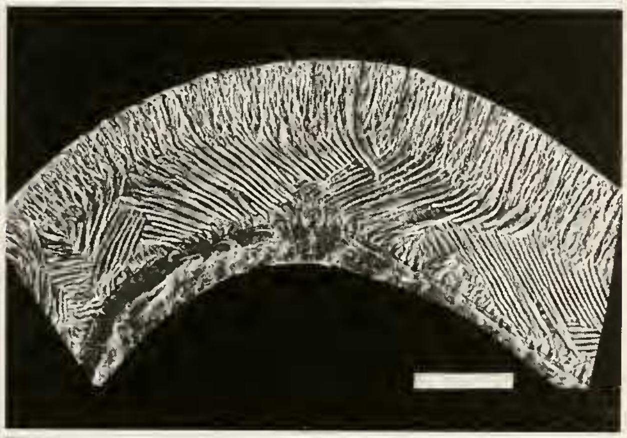
Fig. 8: Occlusal view of the enamel band in the leading edge of M_1 of *Microtus juldaschi* demonstrating the crack stopping mechanism in lamellar enamel. A vertical crack runs throughout the thickness of the radial enamel but it is stopped/diverted by prisms of lamellar enamel.. Note the orientation of lamellar enamel prisms making an angle with the crack orientation. Bar = 5 µm.

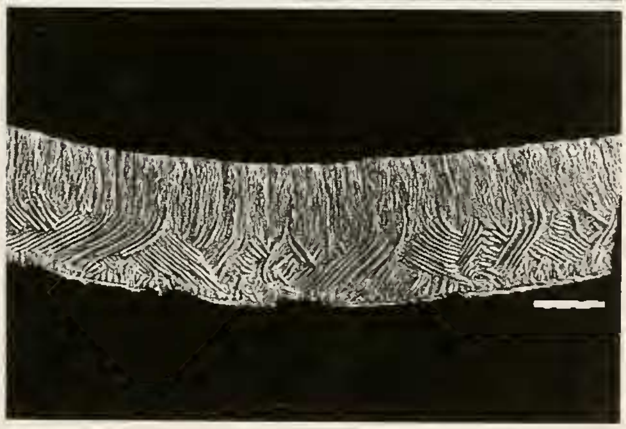
comparatively less developed in *M. sikimensis* compared to that in *M. juldaschi* (figs. 9 & 10). It occupies about 30-55% of the total enamel thickness on synclines (KOTLIA & SAHNI, 1993).

The vertical cracks in *M. sikimensis* are very effectively stopped at lamellar enamel. Fig. 11 shows several hairline cracks on the anticlinal area. The vertical hairline cracks enter only in the radial enamel. In lamellar enamel either they are stopped or they take the direction of lamellar









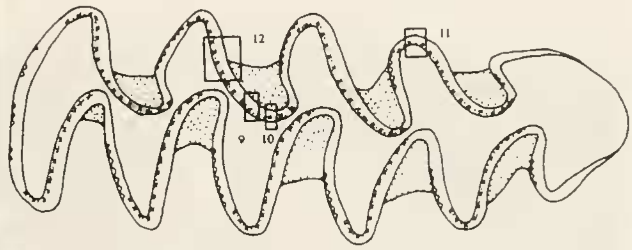


Fig. 9: Occlusal view of the enamel band in the leading edge of M_1 of *Microtus sikimensis*. The lamellar enamel extends more deeply in the leading edge. Several hairline cracks are propagating in the radial enamel; They are split up by HSBs and their direction is changed as they enter lamellar enamel. Bar = 30 µm.

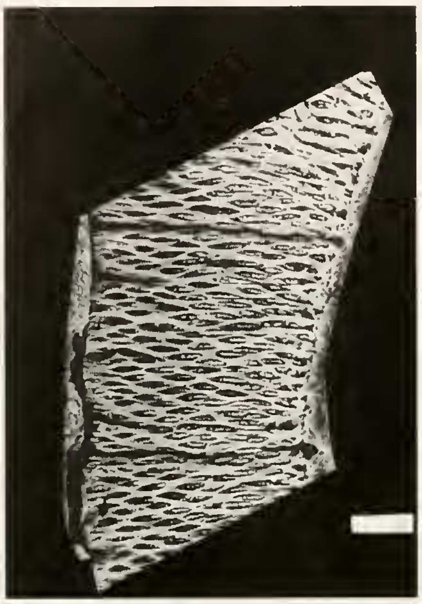
Fig. 10: Occlusal view of the enamel band in the leading edge in M_1 of *Microtus sikimensis*. Lamellar enamel occupies about 50% of the total enamel thickness. Bar = 30 µm.

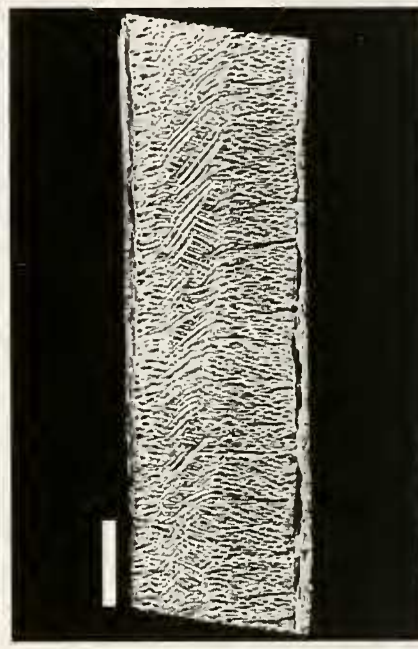
Fig. 11: Occlusal view of the enamel band on an anticline of M_1 of *Microtus sikimensis*. The lamellar enamel occupies about 70% of the total enamel thickness. The lamellar enamel extends for some distance into the trailing edge also. The cracks travel throughout the radial enamel; they change their direction of propagation as they enter the lamellar enamel. In lamellar enamel the cracks follow an interprismatic path in the direction of prism orientation. Bar = 30 µm.

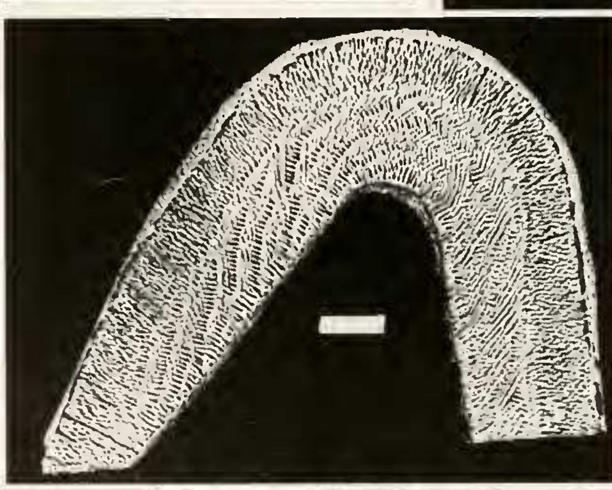
Fig. 12: Occlusal view of the enamel band in the leading edge of M_1 of *Microtus sikimensis*. Radial enamel and lamellar enamel occupy 50% of total enamel thickness. Several hairline cracks are effectively stopped by lamellar enamel but they cross the entire width of radial enamel. Bar = 30 µm.

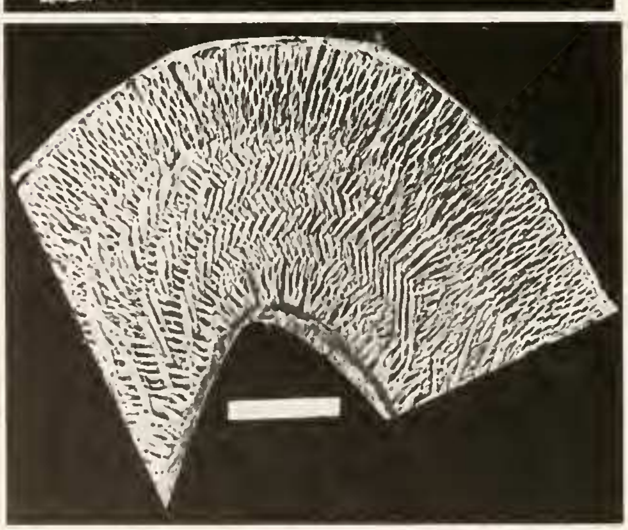
enamel prisms' bands (figs. 9 – 12). In lamellar enamel, prisms of one HSB are at a right angle to the neighbouring band. Therefore the hairline cracks do not cross one band and stop soon. This leaves the enamel least damaged and best protected from such cracks. In figs. 9 & 10, various hairline cracks are seen on the syncline area. Inner lamellar enamel HSBs help in stopping these cracks travelling deep down into the lamellar enamel from outer radial enamel.

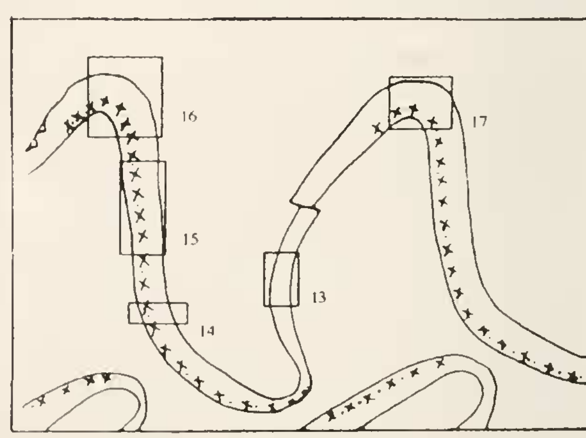
In *Alticola roylei*, the lamellar enamel is highly developed and modified on the apex of dentine triangles and leading edges. It occupies more than three-fourth of total enamel thickness; the remaining one-fourth is occupied by radial enamel.











The cracks as can be seen in figs. 13 –18, pass throughout the radial enamel without much deflection from their initial path but as they reach the lamellar enamel they are stopped by decussating prisms (figs. 14 – 18). This mechanism has been found to be better developed in *Alticola roylei* compared to those in other arvicolids.

During mastication most of the load is taken by the enamel, hence the crack (as seen in the centre of fig. 18) originating from dentine is not possible, because to develop such cracks masticatory forces have to be applied on dentine which is very unlikely. Besides, most of the premortem cracks do not penetrate the dentine because the tensile strength of dentine is somewhat more than that of enamel (WATERS, 1980; RENSBERGER, 1987). This crack was created artificially during polishing. In fig. 19, several hairline cracks are seen originating from outer radial enamel. As soon as these cracks reach lamellar enamel they get bifurcated in a 'Y' shaped pattern and stop.

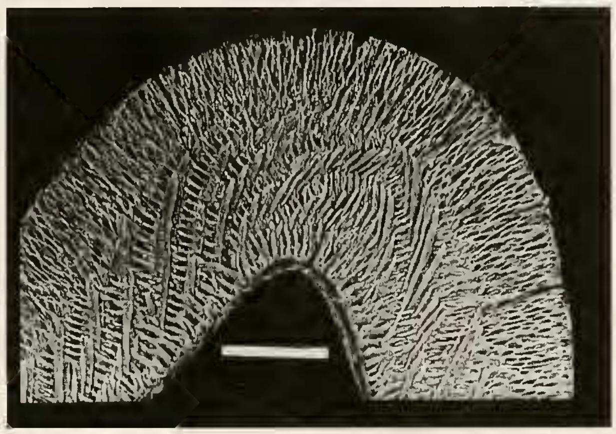


Fig. 18: Occlusal closer view of fig. 16 showing more clearly the orientation of cracks and HSBs in lamellar enamel. Bar = 30 µm.

Above observations suggest that the lamellar enamel plays an important role in the molars of arvicolids for stopping the vertical cracks in most effective manner. The presence of lamellar enamel is a derived condition in arvicolid molars and that is highly developed in *Alticola roylei* and *Microtus* and is comparatively less developed in *Kilarcola indicus*.

Fig. 13: Occlusal view of the enamel band in the trailing edge of M_1 of *Alticola roylei*. The entire trailing edge is dominated by radial enamel. The vertical cracks travelling through the enamel width remain unaffected. The radial enamel fails to stop these cracks and they damage the entire enamel width up to the enamel dentine junction. Bar = 10 µm.
Fig. 14: Occlusal view of the enamel band in the leading edge of M_1 of *Alticola roylei* showing crack stopping mechanism in lamellar enamel. A vertical crack is travelling throughout the thickness of the outer radial enamel, but at the boundary of radial and lamellar enamel the crack is being stopped by the decussating HSBs of lamellar enamel. The prisms of HSBs of lamellar enamel make an angle with the direction of the crack. The crack is getting diverted into another direction from its original direction of propagation. This crack looses its intensity due to a change in its original direction of propagation and stops soon. Bar = 10 µm.
Fig. 15: Occlusal view of the enamel band in the leading edge of M_1 of *Alticola roylei*. Lamellar enamel occupies more than half of the total enamel thickness. Several vertical hairline crtacks travelling across the radial enamel are being stopped at the junction of radial and lamellar enamel. Bar = 30 µm.
Fig. 16: Occlusal view of the enamel band on the anticline of M_1 of *Alticola roylei*. The radial enamel occupies about outer 30% and lamellar enamel occupies inner 70% of the total enamel thickness. Bar = 30 µm.
Fig. 17: Occlusal view of the enamel band on anticline of M_1 of *Alticola roylei* showing propagation and extension of several hairline cracks. Bar = 30 µm

Functional Interpretation

A number of cracks and their definite patterns have been observed in the first lower molars of arvicolid genera e.g. *Kilarcola indicus, Kilarcola kashmiriensis, Alticola roylei, Microtus juldaschi* and *M. sikimensis*. Earlier studies have suggested that the HSBs have evolved to resist the propagation of cracks which make an angle with the HSBs (Rensberger & Pfretzschner, 1992). In arvicolid molars, maximum load during chewing process is taken by leading edges (Koenigswald, 1982), which may cause tensile stresses, mostly around leading edges and molar anticlines. These stresses seem to be responsible for producing cracks in the enamel. The orientation of these cracks would be at right angles to the direction of major tensile stresses.

The vertical cracks, which are studied in the present work run across the enamel width in all the studied genera of arvicolid rodents.

In *Kilarcola indicus*, we observe that the cracks travel throughout the width of the radial enamel (fig. 2), but stop at discrete lamellar enamel where they meet the decussating prisms of the HSBs due to change in the direction of their propagation (Koenigswald et al., 1987). In fig. 1, a crack is seen origniating from inner side of enamel i.e. from dentine side, this condition is not possible during mastication in natural condition (these cracks were created artificially during polishing process). In *Kilarcola indicus sahnii*, the cracks travel throughout the thickness of radial enamel and are stopped only in discrete lamellar enamel which is the very thin innermost enamel band present mainly on molar anticlines (fig. 3).

In *Kilarcola kashmiriensis*, the cracks travel throughout the width of the radial enamel and bifurcate as soon as they reach the lamellar enamel (fig. 4). This condition is better seen in *Microtus* and *Alticola* (figs. 6 – 9). At the boundary of radial enamel and lamellar enamel, the cracks run parallel to the prisms and choose a direction of lamellar enamel bands leaving a typical 'Y' shaped pattern. The branches of such cracks are inclined to the tension forces and therefore stop soon (Koenigswald et al., 1987). This suggests that lamellar enamel produces the best reinforcing structure against the tensile stresses and plays an important role in resisting the cracks.

The prisms fibres (apatite crystallites) in single prism units are well developed and compactly arranged in lamellar enamel of *Microtus* in comparison to *Kilarcola*.

An increase in the thickness of lamellar enamel a decrease in the thickness of radial enamel (lower external index) has been observed in M_1s of *Microtus juldaschi* and *M. sikimensis* in comparison to *Kilarcola indicus*. If we observe an average development of lamellar enamel on molar anticlines and leading edges of M_1s of various arvicolid genera, we notice that in *Kilarcola indicus*, the lamellar enamel in form of discrete lamellar enamel, occupies about 40% of the total enamel thickness. In *K. kashmiriensis*, the lamellar enamel occupies about 60% of the total enamel thickness and it shows a better development of the lamellar enamel compared to that in *K. indicus. K. indicus* has been considered to have been evolved from European *Cseria* (a subgenus of *Mimomys*) which shows an identical enamel pattern on leading edge and molar anticline (Kotlia & Sahni, 1993; Kotlia, 1994). On further advancing in the phylogenetic sequence of arvicolids, we observe that in extant species of arvicolids, i.e., in *Microtus juldaschi* and *M. sikimensis*, the lamellar enamel occupies on an average around 65-70% of the total enamel thickness. In another species, e.g., *Microtus deterrai* (0,4 Ma) the lamellar enamel occupies about 75% of the total enamel thickness around leading edge and molar anticline (Kotlia & Sahni, 1993). In another extant species of arvicolid, i.e., *Alticola roylei*, we observe that the lamellar enamel occupies about 70-75% of the total enamel thickness. In some other extant species, e.g., in *Arvicola terrestris* and *Clethrionomys glareolus*, lamellar enamel on leading edge has been found occupying about 70% of the total enamel thickness (Koenigswald et al., 1994).

Fig. 19: Occlusal view of polished and etched enamel band in *Alticola roylei*. The thickness of lamellar enamel gradually decreases from the leading edge to the trailing edge. The lamellar enamel occupies about 70% of the total enamel thickness on molar anticline and the leading edge; it extends for some distance into the trailing edge also where it occupies about 30-40% of total enamel thickness. The trailing edge is 100% occupied by radial enamel. Several hairline cracks extend throughout the thickness of enamel in the trailing edge but in the leading edge and the anticline these cracks travel only across the radial and stop as soon as they enter the lamellar enamel. Bar = 30 μm.

In a few other less derived forms like *Prometheomys*, lamellar enamel is found to be poorly developed. It is better developed in other derived forms, e.g., *Kalymnomys* (Koenigswald et al., 1994). In recent *Blanfordimys afghanus*, lamellar enamel is found to be occupying about 70-80% of the total enamel thickness but in an exceptional case, *Ellobius fuscocapillus* possesses weakly developed (primitive) Schmelzmuster. It has only discrete lamellar enamel in its anticline. This genus still survives probably because it occupies a very specialised ecological niche (Koenigswald, 1980; Kotlia & Sahni, 1993).

From our studies it is clear that the increase of the width of lamellar enamel and decrease in the width of radial enamel through time (i.e. from *Kilarcola indicus*, 2,4 Ma to *Microtus* and *Alticola*, recent), is an evolutionary feature which provides best reinforcement against the vertical hairline cracks and allows arvicolid rodents to use new types of food and increase their dietary diversity.

The above observations suggest that the radial enamel in which the prisms are arranged in steep angle to the horizontal chewing surface, fails to stop vertical cracks parallel to the chewing surface. Radial enamel provides the best reinforcement against abrasion. It is demonstrated that when the chewing forces and prism directions are parallel, a higher resistance is provided; the resistance decreases with the increase of the angle between enamel prisms and chewing forces (Rensberger & Koenigswald, 1980; Koenigswald & Clemens, 1992). Radial enamel is found to be more developed quantitatively in *Kilarcola indicus* and *K. kashmiriensis* whereas in the later forms, e.g., in *Alticola* and *Microtus* it is highly developed on the push sides and least developed on the pull sides of cutting edges (Koenigswald et al., 1994).

Conclusions

Enamel microstructure in arvicolid molars (especially in M_1s) is characterised by (Koenigswald, 1990: Koenigswald & Martin, 1984):

a, Outer radial enamel.

b Inner decussating lamellar enamel on apices of dentine triangles, leading edges and around the *Mimomys*-Kante.

c. Inner tangential enamel on the trailing edges.

An increase in the thickness of lamellar enamel and decrease in the thickness of radial enamel is observed in the M_1s of arvicolids through time. The thickness of lamellar enamel is minimum in *Kilarcola indicus* and maximum in *Microtus juldaschi*. The radial enamel in *Kilarcola indicus* and *K. kashmiriensis* is more developed whereas in later forms, e.g., *Alticola* and *Microtus* it is highly developed on the push sides and least developed on the pull sides of cutting edges.

The lamellar enamel produces the best reinforcement to hinder the vertical cracks. The radial enamel is least effective in stopping these cracks and is highly resistant to abrasion (Koenigswald & Rensberger, 1980; Fortelius, 1984, 1985), These are the evolutionary features among the arvicolids and may be related to a 'more advantageous Schmelzmuster' in younger aged arvicolid rodents having optimal quantity of radial enamel to compensate for the high abrasion and lamellar enamel to hinder vertical hairline cracks. The hypsodont (high crowned) molars of arvicolid rodents having optimally developed radial enamel and lamellar enamel in later arvicolid genera seem to allow them to feed of some kind of new kind of food habit with increasing their dietary diversity.

Acknowledgements

The authors are grateful to Prof. Ashok Sahni (CAS in Geology, Panjab Universiy, Chandigarh) for reviewing the manuscript and offering valuable suggestions. Financial assistence provided by DST in the form of Young Scientist Project (SR/SY/A-09/94) to RS and by UGC to BSK is gratefully acknowledged. Various laboratory facilities were provided by the Head, Geology Department, Lucknow University.

We gratefully acknowledge the thoughtful reviews and fruitful comments provided by the reviewers.

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